

Premature opening and dimorphism in *Hakea decurrens* (Proteaceae) follicles: a bet-hedging regeneration strategy?

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Abstract

Hakea decurrens (Proteaceae) is generally regarded as a strongly serotinous species, with woody follicles opening only after fire; however, field observations indicate that follicles do open in the absence of fire. This study examined whether premature follicle opening served as a bet-hedging regeneration strategy, by which plants could recruit during protracted inter-fire periods. Two follicle morphs were identified: a thinner 'slug', and a thicker, more robust 'snail'. 'Slug' morphs were always observed open, while 'snail' morphs varied in the proportion of open follicles across several study areas with differing time-since-fire, highlighting a moderate correlation between the number of open 'snail'-shaped follicles and older trees. The proportion of open follicles was compared with that of *Hakea eriantha*, a species which occurs in very similar vegetation types to *H. decurrens*. Fewer open follicles were observed in this species. There was no sign of successful *H. decurrens* recruitment during inter-fire periods, indicating that premature follicle opening is not reproductive bet-hedging. Lack of inter-fire recruitment, as well as observations of webbing and insect larvae within a majority of 'slug' follicles, led to the formation of a new hypothesis which highlights seed abortion and granivory as potential key drivers behind follicle dimorphism and premature follicle opening in *H. decurrens*. (*The Victorian Naturalist* 132 (5) 2015, 139–146)

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Introduction

Serotiny has evolved independently and repeatedly in a number of widely separated plant taxa (Simon *et al.* 2009). In serotinous species, plants retain their seeds within protective woody fruits or cones in the canopy, delaying seed release until triggered by an environmental stimulus (LeMaitre 1985; Midgley and Enright 1999). Serotiny is a convergent plant trait thought to be influenced by selective forces such as fire, soil nutrient availability, and seed predation (Clarke *et al.* 2012). Within a single plant community, the degree of serotiny can differ between species, and sometimes even within species, typically dictated by the environmental gradients along which these individuals might occur (Enright and Goldblum 1998). Weakly serotinous species tend to retain seeds for shorter periods and release seed spontaneously in comparison to their strongly serotinous counterparts. Some strongly serotinous species can open follicles upon reaching reproductive maturity after five years (Groom and Lamont 1997), although most tend to retain their seed

for periods upwards of ten years—sometimes indefinitely if external triggers are absent or fail to cue seed release. Strong serotiny is a trait synonymous with obligate pyriscence (Lamont *et al.* 1991), and tends to lead to trade-offs in seed production, resulting in fewer seeds per follicle (Cramer and Midgley 2009).

Varying degrees of serotiny are expressed in the genus *Hakea* (Groom and Lamont 1997), with some species believed to recruit only after fire as obligate reseeders. *Hakea decurrens* and *Hakea eriantha* are two such reseeding species that rely entirely on seeds stored within their canopy seed banks for post-fire recruitment (Enright and Goldblum 1998). As both species are typically thought to be strongly serotinous, these species are vulnerable to local extinctions if fire intervals are shorter than the time taken for them to reach reproductive maturity (Bradstock *et al.* 1997; Ooi *et al.* 2006). Interestingly, follicles of *H. decurrens* appear dimorphic, present as either 'slug' or 'snail' morphs (Fig. 1), and open follicles have often been observed in

the absence of fire. It is unclear why two follicle morphs exist; this may be associated with an alternative recruitment strategy, where some seeds are released during protracted inter-fire periods. This would, in turn, indicate a lesser degree of serotiny in *H. decurrens*. However, it is also possible that seeds are merely being aborted early.

Enright and Goldblum (1998) recorded instances of inter-fire recruitment within *H. decurrens* stands where time-since-fire was between 24 and 28 years. A correlation was found between older stand ages, greater instances of adult mortality, increased seed release and the incidences of severe drought (Enright and Goldblum 1998). This leads to the possibility that environmental stresses other than fire (such as drought, disease and senescence) may play a role in inter-fire recruitment, which is a potential indication that *H. decurrens* may employ a 'bet-hedging strategy', commonly witnessed in 'weakly serotinous' species (Lamont *et al.* 1991), in order to maintain population numbers during protracted inter-fire periods (Clarke *et al.* 2012; Whelan *et al.* 1998). However, successful seedling establishment may not always occur during cases of extreme environmental circumstance or stress (Groom and Lamont 1998).

In order to determine whether a bet-hedging strategy is indeed at play, this study aimed to quantify the degree of inter-fire recruitment of both *H. decurrens* and *H. eriantha*—two obligate reseedling species that occur in the Cape Conran hinterlands of East Gippsland, Victoria. It was predicted that bet-hedging would increase as time-since-fire increased, and consequently more follicles would be open on older plants. This study also aimed to discover if follicle dimorphism and premature follicle open-

ing in *H. decurrens* was a component of this bet-hedging strategy. The expectation was to observe a difference in the proportion of open and closed follicles between 'slug' and 'snail' morphologies.

Methods

Study Species

This study focused on two native, strongly serotinous and obligate reseedling members of the Proteaceae family: *Hakea decurrens* subsp. *platytaenia* and *Hakea eriantha*.

There are currently three subspecies recognised under *Hakea decurrens*. These are *H. decurrens* subsp. *decurrens*, *H. decurrens* subsp. *physocarpa*, and *H. decurrens* subsp. *platytaenia*—spanning the dry sclerophyll forests, woodlands and heaths of New South Wales, Victoria and Tasmania on sandy and rocky soil (Barker *et al.* 2000). The subspecies of focus within this study, *H. decurrens* subsp. *platytaenia*, is present along the coastal heathlands of eastern Victoria, south-east NSW and the Bass Strait Islands (Barker *et al.* 1995), and appears as a spreading shrub or small tree up to 5 m in height. This species produces ovoid horned and beaked follicles which appear dimorphic, with individual follicles found to vary between 18 to 35 mm in length and 14 to 36 mm in width on a single plant (Barker *et al.* 2000). Plants become reproductively mature at three years and senescence begins at approximately 24 years (Enright and Goldblum 1998).

H. eriantha is a less widespread species, restricted largely to wet sclerophyll forests and woodlands of coastal New South Wales and Victoria. Plants range from shrubs to trees of 10 m high and produce smooth beaked oblong-ovoid follicles 20 to 30 mm long and 15 mm wide (Barker *et al.* 2000), which closely resemble *H. decurrens* 'slug' follicles. Outside Victoria, *H. eriantha* also has been recorded as lignotuberous (Baker *et al.* 1996).

Study Sites

In order to compare the degree of inter-fire recruitment occurring in different-aged stands of *H. decurrens*, four areas with differing time-since-fire (1981, 2001, 2005 and 2010—known year of last burn) were identified in the Cape Conran hinterlands of East Gippsland, Victoria



Fig. 1. Sketch of *Hakea decurrens* follicles, showing a 'slug' (left) and 'snail' (right). The follicles of *Hakea eriantha* resemble the 'slug' morphology of *Hakea decurrens*. (Scale: x1.1 magnification).

(Fig. 2). The *H. decurrens* subsp. *platytaenia* sites were located along Marlo–Cabbage Tree and Cabbage Tree–Conran Roads, all roughly within 2 kilometres of one another, while the *H. eriantha* site was located along Palm Track, approximately seven kilometres north-west of the other sites.

The Cape Conran area has a mean minimum annual temperature of 12°C and a mean maximum of 19°C, and receives an average of 964 mm of rainfall per year (Bureau of Meteorology 2014). Soil types found within the coastal park are generally sandy in areas that support forest vegetation (Cape Conran Coastal Park Management Plan 2005).

Sampling Method

Within each of the four fire histories, 10 *H. decurrens* plants were selected randomly by blindfolding and disorientating a researcher, and then having them select a random direction in which to locate the nearest plant. Of the 10 plants selected within each fire zone, the first five were used to mark the centre of a circular quadrat with a radius of 1.5 m. The basal trunk diameters of all conspecific saplings and trees within this area were measured to evaluate the extent of recruitment in the absence of fire.

Basal diameter has been considered a reliable proxy for assigning plant age classes (Perryman and Olson 2000).

Each of the ten randomly selected focal plants per fire zone was used to assess the extent of follicle opening in the inter-fire period. All follicles (or up to 100 on older plants) were counted to determine the proportion of open versus closed follicles per tree. Due to the appearance of follicle dimorphism in *H. decurrens*, each follicle counted as either open or closed was also scored as either a 'slug' (a thin and small follicle) or a 'snail' (robust and comparatively large) (Fig. 1) in order to assess whether one morph was more likely to open than the other in the absence of fire.

In order to explore whether the degree of inter-fire recruitment is variable within the genus, a stand of *H. eriantha*, unburnt since 1981, was visited to compare against the *H. decurrens* stand of the same age. *H. eriantha* was chosen as a suitable comparative species in this study because it is also an obligate reseeder and occurs in the same coastal heath and woodland environment as *H. decurrens* (National Herbarium of NSW 2014); however, it does not exhibit the same 'slug'/'snail' follicle dimorphism. The



Fig. 2. Map of Cape Conran fire history. Dots represent study sites of four different fire zones (1981, 2001, 2005 and 2010) for *Hakea decurrens* and one *Hakea eriantha* (1981). (Map source: DEPI).

proportion of open and closed follicles of the 10 *H. eriantha* plants was scored in the same manner as *H. decurrens*.

Statistical Analysis

T-distribution confidence intervals were calculated for the proportion of open 'slugs' and 'snails' at each fire site, and in *H. decurrens* and *H. eriantha* in total. The correlation between basal diameter and number of open follicles of *H. decurrens* was examined using linear least squares to produce a line of best fit.

Results

'Slugs' were always open at all sites (Fig. 3). The 1981 fire cohort had a statistically significantly higher proportion of open 'snails' than the 2001 and 2005 cohorts; all other differences were not significant. A trend of increasing proportion of follicles open with increasing time-since-fire was observed, except in the 2010 site. This is likely due to the smaller follicle sample size, and correspondingly higher variance, in the 2010

fire cohort, in which individual plants carried few follicles.

Size class distributions of *H. decurrens* were narrow. Notably, the 1981 site contained many larger individuals, but no plants with a base diameter less than 10 cm. This indicates pulse recruitment, and thus no inter-fire recruitment in the near vicinity of reproductive plants, despite the opening of follicles (Fig. 4).

There was a trend of increasing proportion of open 'snails' with increasing basal diameter ($R^2 = 0.40$, Fig. 5). This shows a moderate positive correlation, indicating that open 'snails' accumulate over time. A large contribution to the variance came from the 2010 fire site; exclusion of this data would increase the strength of the relationship.

H. eriantha had significantly fewer open follicles than *H. decurrens* (Fig. 6). *H. eriantha* also lacked the differing follicle morphologies found in *H. decurrens*.

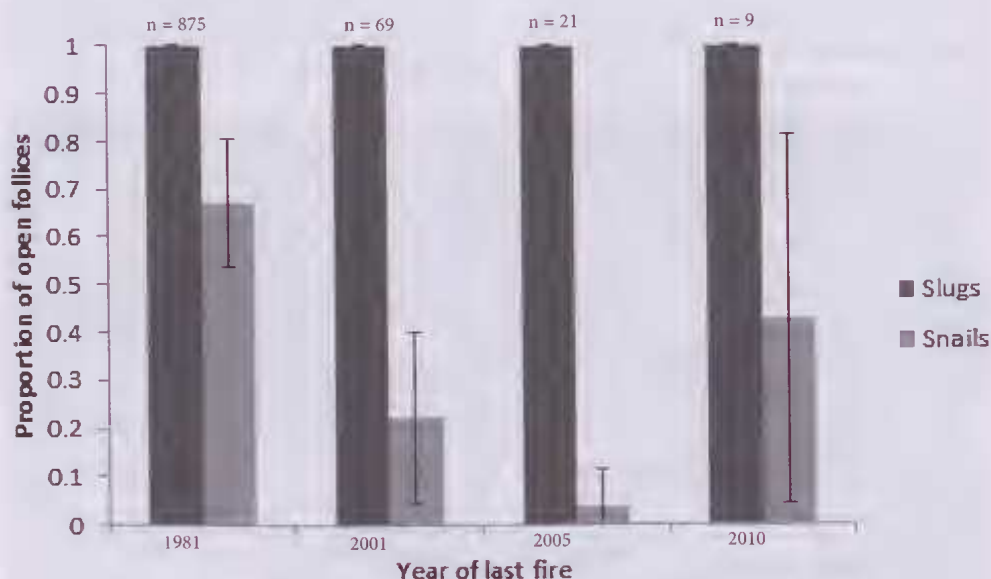


Fig. 3. Proportion of open 'slug' and 'snail' follicles on *Hakea decurrens* in different fire sites. Error bars show the 95% confidence interval. Sample sizes for 'slugs' are 75, 58, 7 and 8 for 1981, 2001, 2005 and 2010, respectively. Sample sizes for 'snails' are 875, 69, 21 and 9 for 1981, 2001, 2005 and 2010, respectively.

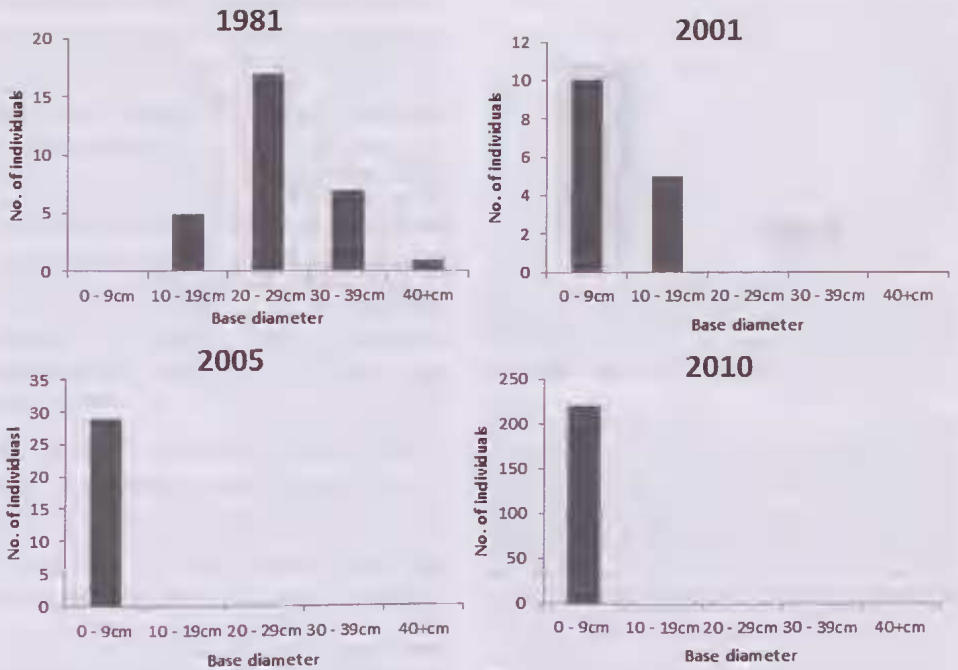


Fig. 4. Size class distributions for *Hakea decurrens* fire sites, showing narrow distributions of age classes.

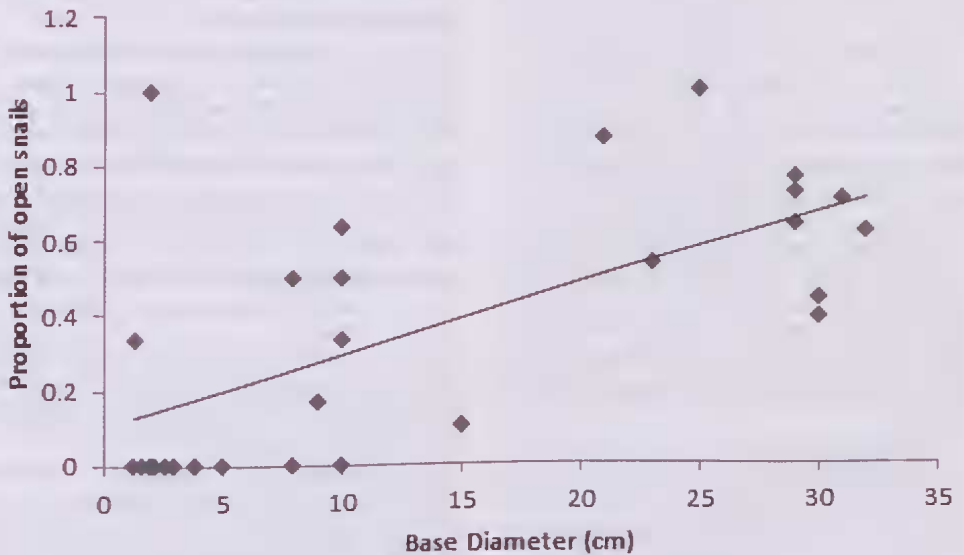


Fig. 5. Proportion of open 'snails' and *Hakea decurrens* basal diameter with line of best fit (least squares). $R^2 = 0.40$.

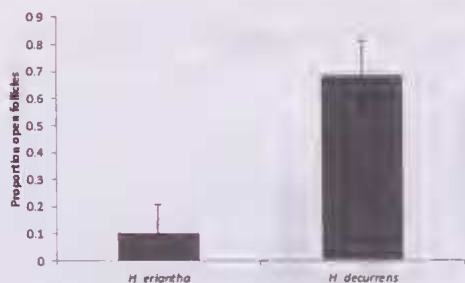


Fig. 6. Proportion of open follicles in *Hakea eriantha* versus *Hakea decurrens*, of the 1981 cohort. Error bars are 95% confidence interval. A total of 383 follicles were examined in *H. eriantha*, versus 1122 follicles in *H. decurrens*.

Discussion

The original premise for this study was to investigate whether bet-hedging was an underlying recruitment strategy driving premature follicle opening in *H. decurrens*. As expected, the proportion of open follicles was found to increase as time-since-fire increased, and there was a significant difference between the proportion of open 'slug' and 'snail' morphs, with 'slugs' open 100% of the time. However, there were no signs of successful recent recruitment in older stands, from which it is inferred that inter-fire recruitment had not occurred in any of the four fire zones. Premature follicle opening thus appears not to be a bet-hedging strategy.

There is an indication that open 'snails' accumulate over time, as the data points to a moderate correlation between the number of open 'snail'-shaped follicles and older plants. In older stands, where these observations were recorded, there seemed to be greater instances of adult mortality and follicles could be expected to open as plants senesce. Fewer open follicles were observed on *H. eriantha* suggesting that, whilst both species are serotinous, the degree of serotiny varies substantially between the two species occurring in very similar vegetation types.

As 'slugs' were always found to be open, it is possible that they represent follicles that were aborted before becoming 'snails'. Plants in the 2010 fire site possessed open follicles of both morphologies, despite being less than four years old. These seeds were unlikely to have lost viability due to age, implying that there must be some other cause of seed leakage.

Groom and Lamont (1997) proposed that strong serotiny in *Hakea* species was linked with significantly thicker and denser follicles than fruits of weakly serotinous species. Whilst this trait was evidently adapted for the protection of seed during fire, it may also confer the additional fitness benefit of reduced seed predation (granivory). Given this hypothesis, it seems reasonable to infer that the more robust 'snail' morphs are the desired adaptive trait in *H. decurrens*, providing protection for seeds within thicker, denser follicles. Midgley (1991), however, argues that follicle size variation is more a product of seed mass within the follicle, which determines the follicle size, and thus the degree of serotiny.

Whilst contentious, there is a convincing body of evidence that indicates granivory is a major driver of serotiny evolution. Bradshaw *et al.* (2011) described the fossil remains of a *Banksia* species from the Oligocene with evidence to suggest that predation by birds, insects and mammals may have been favouring the evolution of woody fruits for millions of years. Observations by Naser (1968) found that moth larvae are more likely to die from predation, starvation and dehydration whilst attacking a strongly serotinous *Hakea* species from the outside. Earlier experimental evidence, collected over three consecutive years by Gordon (1992), described a similar interaction between seed moths and a *Hakea* species. His data indicated that whilst seed destruction may not always be severe, targeted and substantial predation can lead to a reduction in the accumulated canopy seed by up to 64%. As such, Zammit and Westoby (1988) also considered that the increased metabolic cost of producing thick and woody follicles for the protection of nutritious and limited seed in many Proteaceous taxa may account for such a selective pressure, particularly since they believe that the alternative strategy may very likely have resulted in an increased degree of predation within the seed bank.

Consequently, the correlation between thicker, denser follicles and strong serotiny may be explained by granivory pressure. In the case of *H. decurrens*, it seems external seed predation is not the only type of predation occurring. In the field, observations of webbing and the presence of insect larvae within a

large majority of the open 'slug'-shaped follicles led to a new hypothesis: 'slug' morphs are a response to granivory and the result of early seed abortion, whereby the plant cuts its losses after detection of unviable seed, produced when floral infestation by a parasitic insect occurs.

This hypothesis may explain supposed follicle dimorphism and premature follicle opening in *H. decurrens*. True follicle dimorphism in the *Hakea* genus has been described formally only in the locally-occurring *Hakea nodosa*, which produces two distinct follicle morphs, one which remains closed while attached to the bush and the other which opens while still attached (Barker *et al.* 1996). However, signs of invertebrate interference and seed abortion in the case of *H. decurrens* suggest that the so-called dimorphism observed during this study may actually be a symptom of granivory or abortion of seeds. It is still unclear whether the presence of insect larvae within open 'slug' follicles is direct evidence that floral infestation has, in fact, occurred. It is quite possible that 'slug' morphs are merely aborted seeds and as such, follicles open once nutrients from the plant are no longer received, creating suitable habitats for insect larvae after the fact. Nonetheless, the presence of webbing or insect larvae within 'slug' morphs collected or observed in the field remained consistent across all fire zones, leading to the conclusion that granivory is likely occurring, albeit at a much earlier stage of follicle development. The fact that follicle dimorphism does not occur in *H. eriantha* may also indicate that some type of symbiotic relationship may have evolved between *H. decurrens* and the insect species which inhabit 'slug' follicles. However, further studies are required to ascertain whether this is plausible.

Conclusion

As this study was designed to determine whether bet-hedging was a recruitment strategy adopted to maintain population numbers during protracted inter-fire periods, many of the interesting observations from this study still remain untested. Exploring the possibility of early seed abortion or determining whether granivory is the major driver of follicle dimorphism and inter-fire follicle opening is a compelling hypothesis that deserves further consideration in

future studies. A more in-depth study to closely observe 'slug' follicles for the presence of larvae or webbing, as well as genetic analysis of the larvae occupying open follicles, should also be conducted to determine whether the insects targeting *H. decurrens* are a single species or not. A single species or closely related group of insects could expose interesting evolutionary relationships at play. Along with this, a comparative analysis between *H. decurrens* and *H. eriantha* should include the examination of other environmental stresses, such as drought and disease, to determine why such a high proportion of *H. decurrens* follicles are aborted early.

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One Hundred and One Years Ago

Exhibition of wild-flowers

As usual, the October meeting of the Club was devoted principally to the annual exhibition of wild-flowers; but seldom in the long series of displays made by members of the Club have the flowers been representative of such a small portion of Victoria as on the present occasion. Owing to the exceedingly dry winter and spring in the central and northern portions of the State, most of the flowers were obtained from the south and east of the metropolis. A noticeable effect of the dry weather was the poor display of *Tetratheca ciliata*, Pink Eyes, bunches of which usually brighten the exhibitions. Fortunately, fine displays from cultivated plants were made by Mr. J. Cronin, Director of the Melbourne Botanic Gardens; Mr. E. E. Pescott, Principal of the Horticultural Gardens, Burnley; and a smaller number by Mr. Hugh Anderson, of Tooronga House, Hawthorn, which, besides providing exhibits to look at, demonstrated the fact that a large number of our native plants can be successfully cultivated in our gardens if given the necessary attention.

The collection from the Botanic Gardens comprised blooms of fifty species of Victorian plants, among which may be mentioned : — *Leptospermum myrsinoides*, Pink Tea-tree; *Livistona australis*, Australian Cabbage-Palm; *Kunzea cordifolia*, White Kunzea; *Cassia australis*, Southern Cassia; *Callistemon salignus*, Willow Bottle-brush; *Styandra glauca*, Blue Spray; *Calythrix Sullivani*, Grampian Fringe-Myrtle; *Bauera rubioides*, Wiry Bauera; *Prostanthera melissifolia*, Balm Mint-bush; *P. nivea*, Snowy Mint-bush; *Phebalium Billardieri*, Satin-wood Phebalium; *Swainsona Greyana*, Pink Swainsona; *Clematis aristata*, var. *Dennises*, Pink-flowered Greater Clematis; and *Boronia pinnata*, Feathery Boronia.

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